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ZOOLOGICAL SOCIETY OF LONDON.

PAPERS.

1. On the Ciliation of Asterids, and on the Question of Ciliary Nutrition in Certain Species. By JAMES F. GEMMILL, M.A., M.D., D.Sc., F.Z.S.

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(Plates I.–III.* and Text-figures 1 & 2.)

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In studying the development of the common Crossfish, *Asterias rubens* L. (4), I was struck by the constancy and functional importance of the ciliation on the various surfaces (epidermal, endodermal, and enterocœlic) of the larva. The larval ciliation being continued at metamorphosis into that of the starfish, it

* For explanation of the Plates see pp. 18–19.

seemed of interest to investigate the ciliary activities of the adult, especially as considerable attention has been paid of late to the role of ciliation * in other animals, with results of much importance alike as regards physiology and structure.

Of the species available in the Firth of Clyde, *Asterias rubens* L., *Solaster papposus* L., *Porania pulvillus* O. F. M., and *Astropecten irregularis* (Pennant), were selected for particular examination, as belonging to families showing very great divergence in form or larval history.

In the course of the investigation, data were obtained indicating that *Porania* secures a portion of its food-supply by ciliary activity. This fact is of the greatest significance as showing how nutritional continuity could have been maintained in the progress of Asterid evolution, during the transition from a bilateral, ciliary-feeding, pelagic ancestor, through an attached stage allowing the gradual acquirement of radial symmetry, to present-day starfishes which obtain their food-supply wholly or mainly by capture through the agency of the sucker-feet.

I. Ciliary Currents.

1. Methods and Orientation.

The direction of ciliary action on the different surfaces was studied by pinning out fresh living preparations from healthy specimens, in sea-water with fine carmine particles in suspension, and then examining under strong reflected light with the help of a Swift-Stevenson binocular microscope. Occasionally, lamp-black or dead *Echinus* sperm was used instead of carmine. In the case of the ampullæ and sucker-feet the corpuscles of the water-vascular fluid served, under bright illumination, to demonstrate the currents, but the results thus obtained were confirmed by the use of carmine injections.

As regards orientation, the specimens are to be considered as lying on a horizontal surface with the aboral side uppermost. In the text:—

Superior, *upwards*, etc., refer to the aboral, and *inferior*, *downwards*, etc., to the oral aspect or direction.

Centripetal means horizontally towards, and *centrifugal* horizontally away from, the vertical or mouth-anal axis.

Laterally inwards and *laterally outwards* indicate currents at right angles to the vertical mid-radial plane of an arm.

Perpendicular refers to currents rising directly from, *i. e.* perpendicular to, a surface or margin.

Opposite currents starting along a line and passing directly outwards from it are described as *shedding away from* the line in question.

* *Cf.* Carlgren, O., Biol. Centralblatt, vol. xxv. 1905, pp. 308–322 (Actinians, Madreporarians). Orton, J. H., Jour. Mar. Biol. Assn. U.K. vol. ix. 1912, pp. 444–478 (Ascidians, Molluscs); vol. x. 1913, pp. 19–49 (*Amphioxus*, Ascidians, Molluscs); vol. x. 1914, pp. 283–311 (Brachiopods, Polychætes, etc.).

2. External Surface.

Area.	*Description of Current.*
Bottom of ambulacral grooves ...	Centripetal in all; strongest in *Porania* and *Astropecten*, weakest in *Asterias.*
Margins of ambulacral grooves on and between the bases of the ambulacral spines.	Laterally outwards in *Asterias* and *Solaster*; laterally inwards and with marked centripetal tendency in *Porania*; laterally inwards in *Astropecten*, especially in the grooves between the groups of spines.
Lateral aspect of rays	On the whole aboralwards in *Asterias* and *Solaster*; perpendicular * at marginal edge in *Porania*, and sometimes also in *Solaster*; in *Astropecten* running strongly downwards, *i. e.* towards oral aspect of the ray, in the grooves between the large marginal plates.
Aboral aspect of rays	Shedding faintly away from mid-radial line in *Asterias**; aboralwards with centripetal tendency in *Solaster* and *Porania*; in *Astropecten* centrifugal along middle line and slanting laterally outwards to either side.
Interradial surfaces (oral aspect) .	Centrifugal, *i. e.* away from mouth, in *Asterias* and *Solaster*; centripetal, *i. e.* towards mouth, in *Porania* and *Astropecten.* Sometimes in young specimens of the former, and usually in old specimens, there is a small area near the oral angle of each interradius with centrifugal ciliation.
Interradial surfaces (lateral aspect).	Aboralwards in *Asterias* and *Solaster*; oralwards in *Astropecten.*
Interradial surfaces (aboral aspect).	Confused in *Asterias*; centripetal towards anus in *Solaster* and *Porania*; centrifugal in *Astropecten.*
Actinal intermediate areas	These areas are well marked only in *Porania* and there the ciliation is centripetal, *i. e.* towards the mouth.
Aboral aspect of disc	Confused in *Asterias*; centripetal towards ana opening in *Porania*; somewhat confused in *Solaster*, but with slight centripetal tendency towards anal opening; centrifugal in *Astropecten.*
Buccal membrane	Entirely centripetal in *Astropecten*; centripetal except for narrow centrifugal zone at margin of mouth in *Porania*, as also in *Solaster*, but with weaker centripetal ciliation in the latter; centrifugal all over in *Asterias.*
Madreporite	Centrifugal in *Astropecten*; from periphery towards centre of madreporic surface in *Asterias* and contrariwise in *Solaster* and *Porania.*
Gills	From base to summit somewhat spirally.
Spines	From attached to free ends often spirally. The large spines (denticles) projecting oralwards from the interradial angles of *Solaster* are ciliated towards the base on the lower, and towards the apex on the upper aspect. In

* Currents somewhat variable.

Area.	*Description of Current.*
	Porania and *Astropecten* the entire ciliation on these spines is from base towards apex. As a rule, gills and spines set on any surface which causes a definite current are ciliated so as to promote this current for some distance up from their bases.
Sucker-feet..............................	From attached to free ends spirally, but showing irregularities in *Asterias*; ciliation absent or extremely weak in *Solaster, Porania,* and *Astropecten.*
Pedicellariæ	Irregular, but, on the whole, from attached to free ends.
Paxillary spinelets of *Astropecten.*	Weak from base to apex.

General.—There can be little doubt but that all over the surface of the body the ciliary currents subserve local respiratory purposes, a function of much importance in connection with the great superficial nerve-tracts, inasmuch as these tracts cannot readily receive adequate oxygenation from the perihæmal fluid bathing their deep surfaces.

Since the currents along the ambulacral grooves are centripetal (p. 2) fresh water is always being brought along them towards the nerve-ring and centre of the disc. This circumstance may well be of importance during periods when the starfish is stationary, as in feeding, or is wholly or partly buried in sand (*Astropecten*).

Text-figure 1.

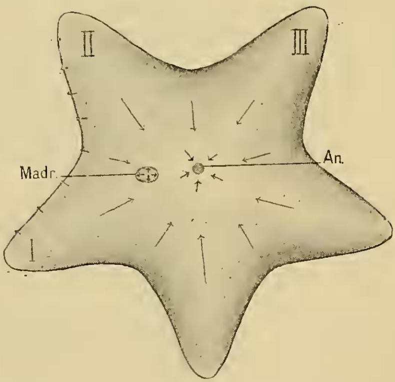


Diagram illustrating the arrangement of the aboral ciliary currents in *Porania.*

An., anus; *Madr.*, madreporite.

We may note that occasionally a number of the papules, instead of showing the usual everted or protruding condition, are found to be introverted (*Porania*). At such times, the spiral ciliation of their epidermal surface keeps this surface bathed with changing water, so that the respiratory function does not completely cease.

The ciliation on all attached or projecting parts (spines and spinelets, pedicellariæ, sucker-feet, gills) is, on the whole, from the attached to the free extremities, an arrangement promoting the removal of débris. In *Porania* and *Solaster*, particularly in the smaller-sized specimens, the skin on the aboral aspect between the gills and spines is ciliated so as to collect particles towards the anus, and throw them up therefrom in a perpendicular stream, from under which the starfish is continually walking away in the ordinary course of its movements. This somewhat remarkable arrangement is illustrated for *Porania* in the accompanying text-figure. In *Asterias*, the skin is too thickly covered with gills, spines, and pedicellariæ to exhibit such an arrangement of currents, but the various structures named serve as the starting-cones of minor ascending currents everywhere on the aboral surface of the disc.

The aboral ciliation of *Astropecten* follows entirely different lines, and is possibly related to ciliary feeding (p. 14). The ciliation on the oral aspect of *Porania* is of direct importance in connection with the last-named function (p. 10).

3 (*a*). Lining of Perivisceral Cavity: Somatopleure.

Area.	*Description of Current.*
Floor of rays in middle line	In *Asterias* centrifugal with irregularities; in *Solaster* centripetal with irregularities; in *Porania* centripetal *; in *Astropecten* very faintly centripetal *.
Floor of rays close to either side of middle line.	Laterally inwards or outwards to or from middle line *; in *Porania* chiefly inwards; in *Astropecten* chiefly outwards.
Floor of rays over ampullæ of sucker-feet.	From base to summit of ampullæ with centripetal tendency, except in *Astropecten* where the tendency is centrifugal.
Infero-lateral angles of rays	Strongly centripetal, providing the chief oralward streams.
Buccal membrane.....................	Centripetal.
Interbrachial septa	Centripetal along inferior angles; centrifugal along superior angles; mixed on sides; tendency * towards circular movement, over the free edges of the septa, in a dextral or watch-hand direction as viewed aborally.
Aboral wall of ray (median portion between the radial cæca).	Strongly centrifugal.
Aboral wall of ray (portions lateral to radial cæca).	Strongly centrifugal and slanting laterally outwards, and then oralwards.
Aboral wall of ray (portions looking into the epigastric cœlomic pockets).	Centripetal in *Asterias* and *Porania* *; mixed in *Solaster* and *Astropecten*.
Lateral wall of ray	Oralwards.

* Currents somewhat variable.

Area.	*Description of Current.*
Aboral wall of disc	Centrifugal interradially, and for the most part radially as well, but sometimes, especially in *Asterias*, centripetal or mixed along the continuations of the epigastric cœlomic pockets.
Aboral gastric ligaments............	Aboralwards.
Oral gastric ligaments	Mixed, chiefly centrifugal.

3 (*b*). Lining of Perivisceral Cavity : Splanchnopleure.

Pharyngeal portion of stomach ...	Aboralwards in all.
Gastric portion of stomach.........	Aboralwards in all.
Pyloric sac............................	Aboralwards in all.
Stalks of radial cæca (except surfaces looking into epigastric cœlomic pockets).	Centrifugal in all.
Surfaces of radial cæca looking into epigastric cœlomic pockets.	In *Asterias* and *Porania* centripetal *; in *Solaster* mixed centrifugal and centripetal.
Oral edges of radial cæca	Centrifugal in all.
Sides of radial cæca	Aboralwards in all.
Aboral edges of radial cæca and outer aspects of epigastric mesenteries.	Centrifugal in all.
Rectal cæca	Centrifugal with spiral currents and mixing, and in some cases a tendency towards circulation in a dextral direction as viewed aborally.
Region of separation between stomachal and pyloric regions of gastric cavity.	* Slight tendency towards circulation in a dextral direction as viewed aborally.
Gonads and Polian vesicles	In general from attached to free extremities, but sometimes spiral or mixed.

General.—Here the primary fact is that the ciliation produces constant and complete mixing of the cœlomic fluid in the interior of the disc and arms. Great centripetal currents flow along the infero-lateral angles of the arms and, reaching the splanchnopleure of the gut-wall, are swept aboralwards and are next driven centrifugally outwards towards the arm-tips by the cilia on the aboral body-wall and on the radial and rectal cæca. There appears to be a certain amount of circular movement on the part of the cœlomic fluid in the dextral or watch-hand direction as viewed aborally. Continual changing of the fluid inside the gills also occurs.

4. Endodermal Lining.

Area.	*Description of Current.*
Pharyngeal portion of gastric cavity.	Aboralwards in all ; in *Asterias* a slight oralward current could sometimes be made out in the middle line of one or other of the interradii, particularly of the anal interradius.

* Currents somewhat variable.

Area.	*Description of Current.*
Stomachal portion of gastric cavity.	Chiefly aboralwards, and strongest along the major radial furrows, but many of the interradial furrows and some of the minor radial furrows show oralward ciliation.
Circular groove between stomachal and pyloric-sac portions of gastric cavity.	Slight tendency to circular movement * in a sinistral direction as viewed aborally.
Pyloric sac, radial grooves	Strongly aboralward or centripetal, *i. e.*, towards the intestinal opening near centre of roof of sac. Note that in *Solaster* each of these grooves (probably through secondary scaling of its edges) forms a canal which opens centrally near the commencement of the intestine, and peripherally near the place of origin of a pair of radial cæca.
Pyloric sac, interradial areas	Diffusely centrifugal, *i. e.*, away from intestinal opening.
Pyloric sac, rosette of minor grooves round opening of intestine.	Centripetal, *i. e.*, towards entrance to intestine.
Stalks of pyloric cæca	Entrance to each pair of cæca is centripetally ciliated all round *.
Roof-grooves of pyloric cæca	Strongly centripetal.
Floor-grooves of pyloric cæca	Strongly centrifugal.
Folded sides of pyloric cæca	Aboralwards, *i. e.*, from floor-groove to roof-groove.
Intestine	From pyloric sac towards rectal sac.
Rectal cæca	Centrifugal, *i. e.*, into recesses of cæca.
Rectum	Not ascertained.

General.—The major result of the endodermal ciliation is to effect sweeping from mouth to anus, but we have also to recognise certain secondary results ensuring: (*a*) mixing and delay within the main gastric cavity, and (*b*) circulation within the cæcal outgrowths. As factors under (*a*), note the oralward ciliation of many of the folds and grooves in the stomachal portion of the gastric cavity, the oralward ciliation of the large interradial areas in the roof of the pyloric sac, and the circular movement (clockwise as viewed from the oral aspect) recognisable near the groove separating the stomachal and pyloric-sac portions of the gastric cavity. The aboralward ciliation of the pharyngeal portion of the gastric cavity will prevent particles from passing out of the gastric cavity during the mixing process. As regards the radial cæca, experiment shows that carmine grains are swept with great rapidity centrifugally outwards from the gastric cavity along their floor-grooves, the streams getting gradually smaller as the apices are neared, since numerous small side-currents pass aboralwards along the walls of the cæcal folds. The last-named currents join the great centripetal stream which passes along the roof-groove of the cæcum and then along the corresponding radial

* Currents somewhat variable.

groove on the roof of the pyloric sac. The circulation within the pyloric cæca seems to depend entirely on ciliary action, contractions of the walls of the cæca either not occurring or being exceedingly slight and irregular.

As regards the rectal cæca, all the ciliary currents appear to be centrifugal, that is, outwards into the lobules. The return currents from the cæca must therefore be passive so far as ciliation is concerned. However, as is indicated below (p. 12), the rectal cæca of *Porania* show rhythmic contractility, while those of *Solaster* and *Asterias*, and probably of other starfishes, are also contractile. The rectal cæca may therefore be emptied or the fluid within them kept from stagnation by the muscular action of their walls.

5. Minor Cavities.

Area.	*Description of Current.*
Dorsal sac	Definitely, but not strongly ciliated. In a particular case (*Solaster papposus*) the current passed sinistrally across the roof, and dextrally* across the floor of the sac.
Axial sinus (general lining).........	On the whole aboralwards, and therefore tending to sweep particles towards the madreporite (see **4**, p. 246).
Pore-canal system of madreporite.	Weakly aboralwards.
Interior of stone-canal	Strongly oralwards (see **4**, p. 269).
Surface of stone-canal looking into axial sinus.	Somewhat indefinite, strongest on the grooves between the calcareous plates of the canal-wall, and following the lines of these grooves, but on the whole with an aboral tendency.
Perihæmal spaces (aboral, oral, circular, and radial sinuses).	Ciliation feeble, flickering, strongest on surface of hæmal tissue; no definite direction of resulting currents noted.
Lining of sucker-feet	Upwards into arm along inner side, *i.e.*, side nearest middle line of arm; downwards towards sucker along outer side, *i. e.*, side furthest away from middle line of arm. Similar currents are found within the ampullæ, *i. e.*, upwards on inner aspect of ampullary wall, laterally outwards within dome of ampulla, and downwards towards sucker on outer wall of ampulla.
Peribranchial spaces and spaces of body-wall.	No ciliary activity made out.

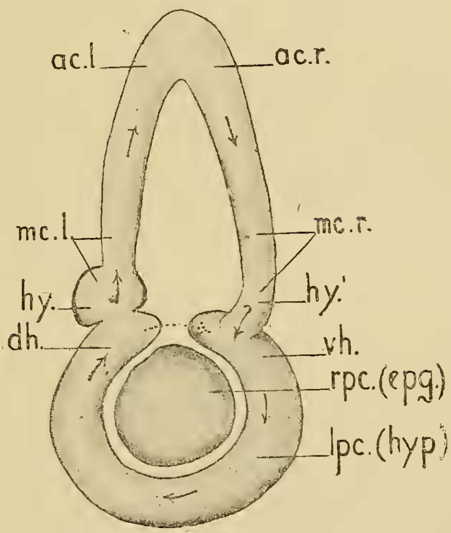
General.—The aboralward ciliation of the lining of the axial sinus is of importance, since by its means particles may be swept from the axial sinus into the stone-canal or the pore-canals (see **4**, p. 270). The fact that the perihæmal spaces are ciliated does not seem to have been previously ascertained. The absence of ciliation from the lining of the peribranchial spaces is a point of considerable interest.

* Clockwise as viewed aborally.

6. Relation of Larval to Adult Ciliation.

While it is true that the larval ciliation passes into that of the adult, the changes in shape and structure which take place at metamorphosis are so profound that in the end only a few details of correspondence between the two systems can be made out. Taking *Asterias rubens* as the type, we note that the oralward ciliation of the circumoral field (food-gathering area, 4, p. 240) in the larva is probably related to the oralward ciliation of the ambulacral grooves in starfish generally and in Crinoids. In further correspondence, we find that the whole or greater part of the buccal membrane in *Astropecten*, *Porania*, and *Solaster* is ciliated towards the mouth. Perhaps the outwardly lashing cilia of the peristomal band (4, p. 239) on the lower lip of the larva may have supplied the basis of the similarly acting cilia at the actino-stomial margin of *Porania*.

Text-figure 2.



Illustrating the circular movement of the cœlomic fluid in the late larva and in the perivisceral cavity of the adult.

ac.l., *ac.r.*, left and right anterior cœloms; *mc.l.*, *mc.r.*, left and right middle cœloms; *dh.*, *vh.*, dorsal and ventral horns of the left posterior cœlom; *hy.*, *hy.'*, hydrocœle, and right hydrocœlic region; *lpc.* (*hyp.*), left posterior or hypogastric cœlom; *rpc.* (*epg.*), right posterior or epigastric cœlom.

Within the perivisceral cavity of the adult, the slight circular dextral movement of the contained fluid appears to be represented in the late larva by a circuit which includes the left posterior cœlom, as well as the left and right anterior and middle cœlomic regions (see 4, p. 245). The left posterior cœlom gives rise to the main part of the adult perivisceral cavity, and in the late larva the circulation of the fluid is from the ventral round to the dorsal horn of the cœlom in question, then through the left and right middle and anterior cœlomic regions back to the ventral horn. At metamorphosis, the dorsal and ventral horns become united and are closed off from the other cœlomic regions named, which for the most part become obliterated, the left middle one, however, giving rise to the hydrocœle. The circuit thus becomes limited to the perivisceral cœlom and the flow is naturally dextral as viewed from the aboral aspect. These points are illustrated in the appended text-figure.

The ciliation of the perihæmal sinuses in the adult is in agreement with the fact of their direct enterocœlic origin.

As regards endoderm, the greater part of the œsophagus of the larva is retained at metamorphosis, and gives rise to the pharyngeal portion of the adult gastric cavity. The larval œsophagus is ciliated towards the stomach, and we note that the pharyngeal portion of the adult gastric cavity is similarly ciliated. Within the stomach of the early larva, food-particles are churned round dextrally as viewed from its anterior extremity (4, p. 240). Something similar occurs within the gastric cavity of the adult (p. 7). In late larvæ, when the stomach has reached full size, oralward currents appear over a large part of its fundus. These are probably represented in the adult by the oralward and centrifugal currents, which one finds on the interradial portions of the stomachal and pyloric sac-regions of the gastric cavity.

II. Ciliation and Feeding.

In Asterids a large part of the actinal epiderm is derived phylogenetically and also in many cases ontogenetically (*Solaster* 2, *Asterias* 4) from the preoral lobe and from the region which in the feeding types of larvæ (*Asterias*) surrounds the larval mouth and includes the circumoral or food-gathering area (4, p. 240). No doubt the bilateral ancestor of Echinoderms obtained its nutriment through ciliary action, as is still done by all feeding Echinoderm larvæ and by the Crinoids. The oral or centripetal currents which one finds in the ambulacral grooves of starfishes are probably of ancestral origin. Recently, certain observations raised the question in my mind whether particular starfishes do not still obtain a portion of their nutriment through ciliary action.

Poranja pulvillus. (Pl. I. fig. 1.)

The observations in question were concerned in the first place with the pin-cushion starfish, *Porania pulvillus* (O. F. M.), their starting-point being the fact that in investigating the actinal ciliation in this starfish with the help of suspended carmine particles, I found that there were periods during which extremely active ingestion of the particles through the mouth into the stomach occurred. The following structural or functional peculiarities in *Porania* next claimed attention. Taken as a complex they seem direct adaptations for ciliary nutrition :—

1. The cilia all over the actinal surface (in ambulacral grooves, round bases of spines bordering these grooves, on actinal intermediate areas, on buccal membrane, and on denticles) act in such a way that streams of particles are continually converging on the mouth-opening.

2. The general shape of the starfish with its large flat intermediate areas, ensures that there is an extensive circumoral ciliated field, adapted for food-gathering purposes.

3. The endodermal ciliation sweeps particles which have entered the mouth into the recesses of the digestive system. We note, in this connection, the aboralward ciliation of the pharyngeal and radial stomachal regions, the centrifugal ciliation of the floor-grooves of the radial cæca, the centripetal ciliation of the roof-grooves of these cæca and of the radial grooves in the roof of the pyloric sac, the aboralward ciliation of the intestine, and the centrifugal ciliation within the interradial cæca.

4. Every specimen of *Porania* that I have watched long enough has shown periods, sometimes lasting several hours, during which at sub-regular intervals the anus opens and a considerable quantity of clear fluid (two to four grammes) is forcibly expelled therefrom. In a particular specimen this occurred, on an average, at intervals of eleven, in another of twenty-five, and in another of forty minutes. Simultaneous observation by means of a suitably adjusted microscope showed that shortly after each expulsion of water from the anus there began a period of active ingestion of carmine particles by the mouth and that this period ceased just prior to the next expulsion.

5. Mucus is secreted by the epiderm of the oral surface and also by the gastric endoderm. To judge by what happens with carmine particles, this mucus is capable of entangling small food-particles, and of so causing the formation of rafts or ropes of nutritive material which travel slowly into the recesses of the digestive cavity.

6. On killing a specimen which had lived for some time in water with an admixture of carmine particles and had exhibited the phenomena described under 5 above, I found carmine particles in the gastric cavity and in the radial cæca. Again, in the case of living specimens which had been "fed" on carmine, abundance of the particles appeared in the fluid expelled from time to time by the anus. In preparations of the living tissues one can demonstrate the readiness with which particles are swept into and out of the radial cæca, collected round the entrance to the intestine, and even (though this occurs less easily) carried along the intestine into the rectal cæca.

7. The interradial or rectal cæca of *Porania* are exceptionally

large, and are present uniformly in all the interradii. They have distinctly muscular walls which contract and expand rhythmically at short intervals, sometimes with such activity as to suggest the systole of the auricular portion of a heart. As observed in living preparations, the contractions do not usually affect all the cæca, or indeed the whole of a single cæcum, at one time, but probably in nature minor contractions of the cæca or of parts of them are continually occurring, serving to cause changing of the contained fluid. It will be remembered from pp. 7–8 that there is no ciliary provision for outgoing currents from the rectal cæca. Presumably, it is the more or less simultaneous contraction of the whole set that produces the periodical expulsion of water through the anus, which was referred to under 4 (p. 11). Turgidity may provide the stimulus to this act. At any rate, simple pressure by the fingers on the aboral aspect of a distended *Porania* will often, after the lapse of a few seconds, induce a perfectly typical expulsion of fluid by the anus. The body-wall in *Porania* is unusually thick and elastic, and when the anus closes these properties may be of use in causing negative pressure within the different parts of the digestive cavity, and thereby aiding the parts to become filled again with fluid entering by the mouth and loaded with particles collected by the actinal ciliation. The interradial or rectal cæca of *Asterias rubens* and of the majority of starfishes are much smaller and less uniform than those of *Porania*. However, alike in *Asterias rubens*, *A. glacialis*, *Solaster papposus* *, and *S. endeca*, these cæca show contractility, and probably have to do with the passage of material along the food-canal and with the evacuation of fæces.

8. After specimens have been deprived of solid food for a time, the addition to the aquarium of finely-divided nutritive material, *e. g.*, débris from the ovary of a sea-urchin, spermatozoa, etc., is almost invariably followed in the course of a few hours by an increase in the weight of the specimen. This increase is lost a day or two after replacement in clean water, and is, I think, to be explained by the taking for the time being of extra fluid into the digestive cavity along with the suspended food-particles. Specimens kept in a glass vessel, through the wall of which their oral surfaces can be observed with the help of a microscope, will often be found to respond to agitation of the water near them by opening the mouth, partially protruding the pharynx, and actively swallowing food-particles. One must exercise much caution in attempting to feed *Porania* with sperm. Individuals, if left too long (24 hours) in a mixture showing only slight milkiness, may distend themselves with water to an extreme degree, sometimes reaching more than twice their former weight. This is usually followed, in my experience, by loss of vitality leading to death within a week or ten days, the sperm or

* See footnote on p. 15.

its products, or simply the great distention, having a markedly injurious effect.

9. If the oral surface of a *Porania* be sharply irritated, the spines at the interradial angles of the mouth will close in and by interdigitating with each other will cover up the mouth-opening completely. In the same way the whole or any part of an ambulacral groove (see Pl. I. fig. 1 *Amb. Gr.'*) can be entirely shut in by the spines on opposite sides of the groove. We seem to have here a ready means of protecting the mouth from exposure to streams of inacceptable or injurious particles.

10. It may be said that all the details given above are to be explained in terms of endodermal respiration. Probably this kind of respiration occurs in our species, as, indeed, it does in other aquatic animals (7). Certainly in captivity *Porania* exhibits remarkable power of healing after injuries to the body-wall. But were internal respiration the only or the principal function, one would expect this function to be cared for in other starfishes, and particularly in such a starfish as *Asterias rubens*, which feeds in the ordinary way far more greedily and must accordingly exhibit far greater tissue change than *Porania*. Yet inward currents of water through the mouth cannot be observed in *A. rubens*, nor does rhythmic expulsion of water through the anus occur. However, for final evidence on the relation of ciliary action to nutrition we must have recourse to observations on the behaviour of *Porania* and other starfishes under circumstances which preclude them from obtaining food by any other means than the action of ciliary currents. Accordingly the following and similar experiments were instituted.

A starfish after being carefully weighed was placed in a bell-jar, the wide end of which was covered by hair-cloth of fine mesh, while the narrow end was connected to a siphoning tube. Next, the bell-jar was immersed in one of a series of tanks with continuous sea-water circulation, and outward siphon action was started by means of the tube from the bell-jar into another tank set lower in the series. Constant change of water within the bell-jar was thereby assured, and at the same time the entrance into the bell-jar of all objects of any size was effectually prevented. At intervals the starfish was taken out and weighed and the interior of the bell-jar cleaned. The first specimen of *Porania* was put in on Feb. 28, 1914. At the end of four and a half months, the mean of several weighings done within the last week of this period was practically the same as the mean of the weighings done in the first week of the period. Thus nothing at all was lost between the end of February and the middle of July, that is, during the period when microscopic food-particles are most abundant in the tanks. Since July there has been some loss of weight, but the specimen is still healthy (October 18). Several other *Porania* similarly treated have remained healthy for almost as long a period, and the smallest of these increased slightly in weight during the months of May, June, and July. In control experiments, specimens of the common Crossfish, *Asterias rubens*, kept under like conditions, lost weight steadily and died, as a rule, in less than eight weeks. We may note in this connection that the sucker-feet of *Porania* are arranged only biserially, and that they are neither particularly strong nor are they kept actively in use. At the Millport Marine Station the *Porania* are never seen feeding on shell-fish etc., or on their neighbours as other species readily do. Yet for several seasons the *Porania* have remained healthy in the tanks as long (nine months or thereby) as circumstances made it convenient to keep them.

In view of the data given under 1–10 above, it is, I think, impossible to escape from the conclusion that ciliary feeding plays a part in the nutritional economy of *Porania*.

Astropecten irregularis (Pl. I. fig. 2).

It will be seen from the details given on pp. 6–7 that the general arrangement of the cilia in *Astropecten* is suggestive of ciliary nutrition. Strong oralward currents run in the ambulacral furrows, being fed by lateral streams coming from the roof and sides of the disc and rays along the grooves between the transverse rows of ambulacral spines. The interradii are powerfully ciliated towards the mouth along avenues bordered by short, thickly clustered spines. The whole aboral surface underneath the great paxillary umbrella has its ciliation so arranged that particles which manage to get through between the tips of the spinelets into the subpaxillary space can hardly fail to be swept ultimately to the mouth-opening, by way of the interradial or the ambulacral grooves. The denticles, or large spines of the interradial angles, are ciliated from base to apex, and frequently project right into the mouth. If a specimen, after removal of the aboral body-wall and the roof of the stomach, be placed mouth downward in a shallow dish of water with suspended carmine particles, a very active upward eddy of particles through the mouth will soon be found to occur. The tube-feet of *Astropecten* are pointed, and the animal habitually crawls on or burrows in sand. It will, of course, find shell-fish and other animals to feed on there, and, as a matter of fact, I have taken out relatively large shells from the stomachs of dissected specimens. But the sand will also contain abundance of microscopic food-particles. The tiny spinelets which make up the paxillæ are weakly ciliated from the base to apex. The conjecture may be hazarded that this ciliation, while keeping out débris, will not prevent the more active microscopic organisms from getting past the spinelets into the subpaxillary space. Once there they will of necessity be swept towards the mouth, and get the chance of passing into the stomach and being entangled in mucus. An anus being absent, waste water would have to escape through the mouth, as occurs in the feeding starfish-larva (4, p. 240). However, I have not yet kept *Astropecten* alive for long periods under the experimental conditions described above in connection with *Porania*; and as regards the ciliation it must be remembered that, in a burrowing starfish, general and local respiration will best be promoted by currents drawn from the aboral surface and the arm-tips.

SOLASTER PAPPOSUS, and OTHER STARFISHES.

S. papposus has powerful sucker-feet, the bi-serial setting of which is more than compensated for by the increased number of the rays. It feeds readily on almost any kind of animal food, and in general the ciliation on the oral aspect, except in the ambulacral grooves, is away from the mouth. However, these grooves are numerous: an oralward current sets in strongly along each; active ingestion of carmine particles may occasionally be observed to take place; opening of the anus and expulsion of fluid occur repeatedly * at certain times; carmine particles may be present in the fluid expelled, if the specimen has been previously kept in water with this substance in suspension; and, finally, particles of carmine may be found after death in the stomach of a similarly treated specimen. Small Solasters kept under the experimental conditions described in connection with *Porania* lose weight and die off, but not so quickly as similarly-treated specimens of *Asterias rubens*. On the whole, I should judge that while ciliary feeding may, and probably does, occur to some slight extent in the Solasters, it is a side result of other processes which subserve endodermal respiration and emptying of the food-canal.

As regards other starfishes, I have had the opportunity of investigating the ciliation on the oral surfaces of *Asterias rubens*, *A. glacialis*, *A. mülleri*, *Henricia sanguinolenta*, *Asterina gibbosa*, and *Palmipes placenta*. In none of these, however, are there currents towards the mouth except along the ambulacral grooves, and, so far as my experiments have gone, none has approached *Porania* in ability to survive after deprivation of solid food.

Bearing on Phylogeny.

It is generally agreed that the ancestor of Echinoderms was a bilaterally-symmetrical ciliary-feeding pelagic organism, and that radial symmetry was acquired during a stage of fixation.

* In the tanks at the Millport Marine Station, where the Solasters feed freely, the fluid expelled is dark green in colour, and is thrown out with considerable force. In a particular specimen of large size, expulsions were observed to occur at intervals averaging eight minutes during a period of an hour and a quarter, the anus remaining open for from 4 to 6 seconds on each occasion. The first two or three expulsions were powerful, the stream of coloured matter emitted into the water reaching a length of nine inches. Ejection became weaker thereafter, and ceased at the end of the period named. I am indebted for these data to Mr. R. Elmhirst, Superintendent of the Millport Station, and to the Rev. W. Steven, B.A.

The view put forward by Semon (6) that the first Echinoderms were *Pentactula*-like forms (whose nearest representatives are now to be found among the *Synaptidæ*) has proved unsatisfactory on many grounds. If we follow the *Pelmatozoon* theory, of which Bather (1) is a foremost supporter, we must figure the Proto-echinoderm as a Cystid-like animal. But from the embryological point of view, as was first brought out by MacBride, there are strong objections to deriving the Asterids from any form which was or had been attached by the (larval) right or the (adult) aboral aspect, and in his memoir on the development of *Asterina*, MacBride (5, p. 398) put forward the view that the Asteroids and Crinoids separated off from each other as early as the fixed stage of the ancestor.

It seems to me that recent embryological evidence and, in particular, the data from *Asterias rubens* L., strongly support this view, or, at any rate, that part of it which derives the Asterids directly from the fixed ancestor. The larva of *A. rubens* is a feeding bipinnaria, and conforms almost exactly to the conventional *Dipleurula*. It has, as I believe, a primitive circulatory centre (4, p. 273) resembling that found in the Enteropneusts and Pterobranchs, the phyla most nearly allied to the Echinoderms. It develops an attaching organ in the middle line anteriorly, fixes itself, bends leftwards, and gradually acquires radial symmetry. During this process, the larval œsophagus, stomach, and intestine are retained, while the changes undergone by the cœlomic cavities are perfectly simple and direct. The attaching stalk, now connected with the oral side of the disc, becomes separated off after the sucker-feet have acquired adhesive and locomotor functions. On the other hand, the only Crinoid larva we are acquainted with (that of *Antedon*) is quite unlike a *Dipleurula*. It does not feed for itself, and the ontogenetic development of its alimentary canal and cœlomic cavities is very different from any course that could have been followed in evolution. In view of these facts, it seems to me that we are compelled to derive the Asterids from the fixed ancestor directly and not through the intermediary of a Pelmatozoic form. But the acquirement of radial symmetry could only take place during an evolutionary period of great, if unknown, duration, and throughout the later portion of this period the attaching stalk must have been connected with the oral aspect, and this aspect must have been turned towards the sea-bottom or the surface of attachment. The difficulty now presents itself that the characteristic Asterid mode of obtaining food seems incompatible with this kind of fixation. MacBride's suggestion (5, p. 394) that the evolutionary change took place at parts of the sea-bottom, where currents were continually bringing along objects which might be seized upon by the adhesive tentacles, is of too "ad hoc" a nature to be entirely satisfactory without supplemental data. But if we find that ciliary feeding still occurs in an adult starfish, we have a hint of the manner in which nutritional continuity was maintained. The fixed ancestor fed by ciliary activity during the time when it was becoming, and at first after it had become, an Asterid. It is not necessary that an attached ciliary-feeding organism should have its food-collecting area looking away from the surface of attachment. Given an aboral skeleton, the advantage will be the other way so far as protection from enemies is concerned. The softer oral field could be closely appressed when necessary to the surface of attachment through the agency of the adhesive tentacles, which became evolved into the sucker-foot system. "Easing up" from the surface (cf. *Crania*) would allow ciliary feeding at any time. The tentacles might also begin to capture drifted or moving prey, as MacBride suggested. But in any case gradual perfection of the adhesive function of the tentacles would allow atrophy and separation of the attaching stalk, and, with freedom of movement now possible, opportunities for the capture of the larger kinds of food would be vastly increased and would be utilised sooner or later. Ciliary nutrition would thus be first supplemented and afterwards completely (most Starfish), or partially (*Porania*), replaced. It is worthy of note in this connection that the larval history of *Porania*, so far as it is known, exhibits all the primitive characters referred to above in connection with the development of *Asterias rubens*.

Summary.

A. *Ciliary Action.*—The arrangement of the ciliary currents on the various surfaces of four widely different species of Starfishes has been described in detail. This arrangement is constant for all individuals in each of the species, and, except as regards external surfaces, is practically the same in all the species. Everywhere the arrangement has been shown to be explicable by physiological needs. Ciliation in the perihæmal spaces has been demonstrated.

B. *Ciliary Feeding.*—In the case of *Porania pulvillus* a mechanism for ciliary feeding has been shown to exist, and the results of experiment demonstrate that this kind of feeding actually takes place. As regards *Astropecten*, it is only shown, so far, that the arrangement of the actinal and abactinal cilia makes ciliary feeding possible. In *Solaster papposus* ciliary feeding probably takes place, but in an entirely minor degree. The other Starfishes examined gave negative results. The important bearing of the above results on questions of phylogeny is briefly discussed.

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EXPLANATION OF THE PLATES.

Lettering and Signs.

Amb.Gr. Ambulacral groove.
Amb.Gr.' In fig. 1, portion of an ambulacral groove covered in by interlocking of spines (see p. 13).
Amp. ...... Ampulla of sucker-foot.
Cœl. ...... Perivisceral cœlomic cavity.
G. .... Gill.
G.' .... Three inframarginal gills (abnormal) in the *Porania* shown in fig. 1 (see p. 21).
Gon. ...... Gonad.
Gr. ...... Groove separating stomachal from pyloric-sac portions of gastric cavity.
Inf. A. ... Infero-lateral angle of arm.
Int. ...... Intestine.
Ir.S. ...... Interradial septum.
Phar. ..... Pharyngeal portion of gastric cavity.
P.V. ...... Polian vesicle.
Py.C. ...... Pyloric cæcum.
Py.Mes. Space between the two dorsal mesenteries of a pyloric cæcum.
R.C. ...... Rectal cæcum.
Rad.C. ... Radial canal of water-vascular system.
Stom. ...... Stomachal region of gastric cavity.

● Current centripetal and at right angles to plane of drawing.

+ Current centrifugal and at right angles to plane of drawing.

⟶ Current as arrow points and in plane of drawing.

●→ Current as arrow points and in plane of drawing, but with centripetal tendency.

(→) Current as arrow points and in plane of drawing, but with spiral tendency.

PLATE I.

Fig. 1. A specimen of *Porania pulvillus* from the oral aspect, with arrows indicating the direction of the ciliary currents. See description on p. 3 and, in connection with feeding, p. 10. This specimen showed three inframarginal gills (*G.'*), and is therefore so far an exception to the rule that in phanerozonate Starfishes the gills should be confined to the supramarginal surface (see p. 21).

2. *Astropecten irregularis*, with arrows indicating the direction of the subpaxillary ciliary currents on the aboral aspect, and also of the currents in the marginal, interradial, and ambulacral grooves. See description on pp. 3, 14.

Plate II.

Fig. 3. Transverse section (diagrammatic) of arm of *Asterias rubens* L., showing direction of ciliary currents on the various ectodermal, enterocœlic, and endodermal surfaces, and also within the cavities of the sucker-feet and ampullæ. For the sake of simplicity, only one sucker-foot is shown on either side of the middle line. Centripetal (p. 2) currents are marked by dots and centrifugal currents by crosses. Ordinary arrows show currents running in the plane of the paper, that is, transversely to the axis of the arms; while arrows with a dot on the shaft indicate that there is in addition a centripetal tendency. Arrows enclosed in an ellipse indicate currents flowing in the direction to which the arrow points, but tending to take a spiral course.

4. Transverse section (diagrammatic) of arm of *Porania*, showing direction of ciliary currents. The same general explanation applies to this figure as to fig. 3.

Plate III.

Fig. 5. Vertical section of *Porania* passing along one of the arms, and somewhat obliquely across another arm to show body-wall after removal of stomach. As in figs. 3 and 4 the arrows indicate currents approximately in the plane of the paper, while the dots show centrifugal and the crosses centripetal currents. The tendency to dextral movement is indicated by the curved arrows on the edge of the interbrachial septa (pp. 6, 9).

6. Vertical section (diagrammatic) through stomach etc. of *Porania* to show direction of ciliary currents on the endodermal and splanchnopleural surfaces. At the actino-stomial margin the ring of buccal membrane with outward ciliation should be noted.